ON THE FERTILISATION OF FLOWERS BY INSECTS AND ON THE RECIPROCAL ADAPTATIONS OF BOTH

DURING the last ten years, since, by his wonderful work on Orchids,* Darwin anew turned the attention of naturalists to the remarkable connection between the structure of flowers and the insects visiting and fertilising them, many essays on the contrivances of flowers as apparently affording facilities for intercrossing distinct individuals have been published ; but there is no doubt that by far the greatest part of the work on this subject is still to be done. The most conspicuous flowers attracted, of course, in the first place, the attention of inquirers, and much greater pains was taken to show the possibility of their cross-fertilisation by insects than to observe whether self-fertilisation may possibly take place if not visited by insects. Another very obvious deficiency of observations indispensable to be made on the subject in question resulted,—the fertilisation of flowers by insects being studied by botanists but little acquainted with insects. From this cause, for the most part, when flowers were examined as to their intercrossing by insects, no complete observations were made as to the insects themselves which were supposed to visit and fertilise the flowers, and in many cases the agency of insects was over-estimated in consequence of not observing them directly.

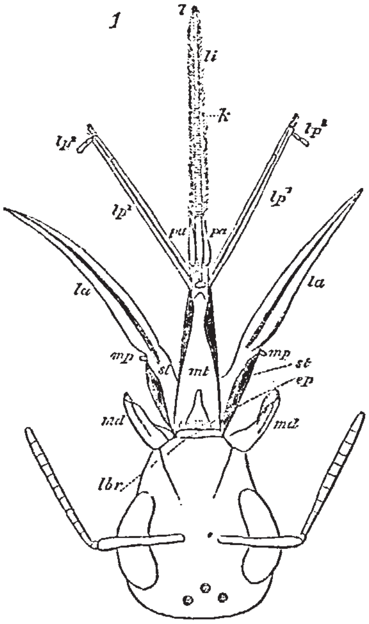

FIG. 1.—Head of a humble-bee (*Bombus muscorum* L. ♀) seen from above, with the oral apparatus stretched out to its fullest extent (5 : 1).

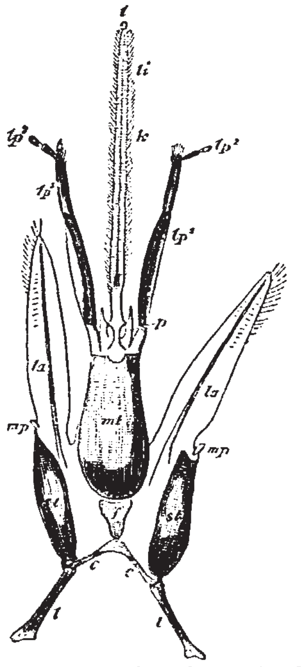

FIG. 2.—Sucking apparatus of a honey-bee seen from beneath (12 : 1)

Therefore, being myself acquainted with our flowers as well as with a great number of our insects, I thought it would be as agreeable as useful if I observed, as far as it was possible for me, the insects which really visit and fertilise our flowers, their adaptations to gain the honey and the pollen, and on the other hand, the adaptations of our flowers to the insects that visit them ; and having during a series of years bestowed all my leisure upon observations of this kind, I put them together in a work which was published some months ago ("Die Befruchtung der Blumen durch Insecten und die gegenseitigen Anpassungen beider." Leipzig, 1873.) Supposing that this book is in the hands of only very few Englishmen, I think it may be of some interest for the readers of NATURE if I make them acquainted with the principal new facts contained in my work, adding some observations made since its publication.

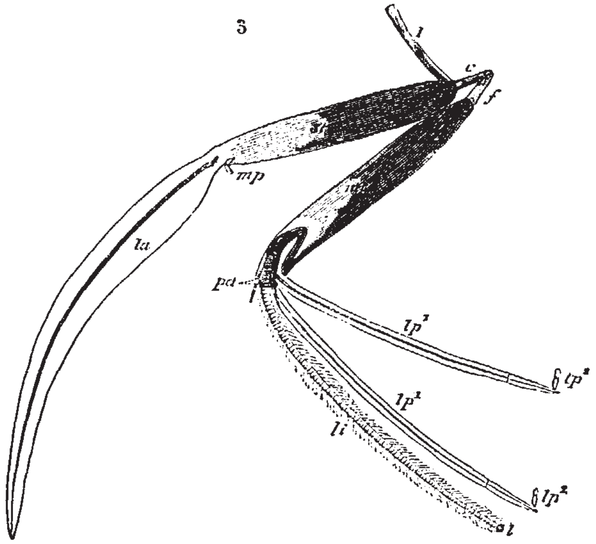

FIG. 3.—Lateral view of the sucking apparatus of a humble-bee (*Bombus silvarum* L.), representing all the four foldings partly commenced, partly imperfectly executed. A piece of the tubular mentum is broken away to show the folding of the base of the tongue (7 : 1).

I.—*In what manner the hive- and humble-bees obtain the honey of the flowers*

The first accurate description and drawing of the parts of the mouth of the hive-bee were given by Swammerdamm about two centuries ago, but he did not succeed in finding out the true function of the tongue ; he described and drew it as perforated at the end,* and believed that it was a simple sucking pipe. His successors saw that the tongue of the bee is by no means perforated at the end, and that fluids, for that reason, cannot enter through its interior, but must be transported to the opening of the œsophagus by the outside of the tongue. Thus with Swammerdamm's error, that the tongue was perforated at the end, the view that it was a sucking organ was also rejected, and since then, even down to our own day, zoologists seem almost unanimously to have denied in general the sucking power of bees. Milne-Edwards calls the Hymenoptera licking insects ("Insectes lécheurs"), and says that the honey-bees nourish themselves not by sucking, but, as it were, by lapping, nearly in the same manner as a cat does ("Ainsi il n'est pas en pompant que l'Abeille se nourrit, mais pour ainsi dire en lapant à peu près comme le fait un chat"). In like manner Carl Vogt expresses his opinion on the same subject, with only the difference that he chooses for the comparison the dog instead of the cat. The bees make use of their tongue to lap, says Carl Vogt, in a somewhat similar manner as dogs apply their tongue to drink ("Sie gebrauchen ihre Zunge etwa in ähnlicher Weise zum Schlappen, wie die Hunde sich der ihrigen zum Saufen bedienen.")[*] Also Claus[†] calls the parts of the mouth of the Hymenoptera biting and licking ("beissend und leckend"), and Gerstaecker blames, in his annual report on the Progress of Entomology, Schenck for describing the tongue of the bees as serving to suck honey, whereas, according to Gerstaecker's opinion, it is only able to lick it. Hence, a good number of our best zoologists absolutely denying the sucking of bees, and our entomological works affording, indeed, very detailed descriptions of the single parts of the mouth of the bees, but not sufficiently accurate ones of the use of them, it may not be fruitless if I explain here, in some detail, the function of the oral apparatus of the bee.

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* "On the various Contrivances by which British and Foreign Orchids are fertilised by Insects, and on the good Effects of Intercrossing." London, 1862.

* "Joh. Swammerdamm, Bibel der Natur. Aus dem Hollandischen übersetzt." Leipzig, 1752. Taf. xvii.

If we stretch out to its fullest extent, as shown in Figs. 1 and 2, the complex machinery of the oral apparatus of a hive- or humble-bee, which, when at rest, is placed by different foldings in an excavation in the under-side of the head, so as to permit but little of it to be seen, the most prominent part we observe is the long vermicular annulated tongue (*ligula*, *li*), at the end of which a little membranous lobe is seen (*l*), the same which was erroneously thought by Swammerdamm to be perforated. The ligula is composed of a great number of rings, each of which is provided with a whorl of hairs; each whorl of hairs can be erected at will by the bee and pressed close to the ligula. The base of the ligula, which bears two appendages, the *paraglossæ* (*pa*), is inserted, together with them, in the tubular *mentum* (*mt*), and can be drawn back, as Fig. 3 shows, into the extremity of the tubular mentum, so that only the tips of the paraglossæ are visible. On both sides of the ligula we observe, also inserted in the mentum, the two four-jointed *labial palpi* (*lp*), the two first joints of which (lp^1), being flattened and very slender, with a central rib, form a sheath to the tongue, enclosing it from beneath, whilst the two minute joints at the tip of the labial palpi (lp^2) serve as feelers.

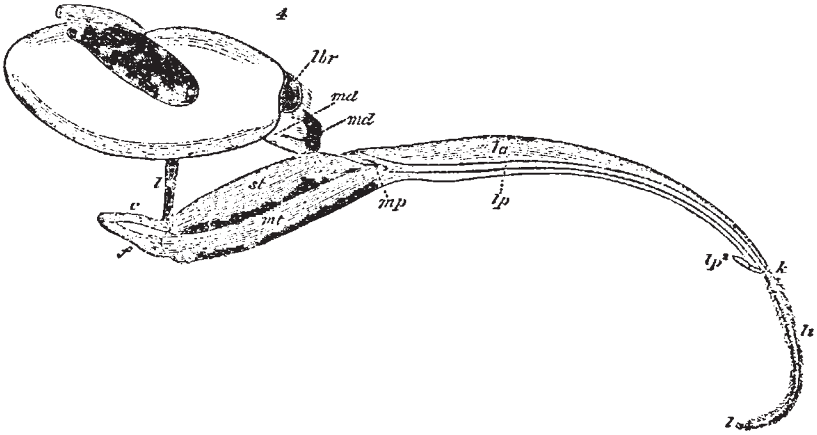

FIG. 4.—Lateral view of the sucking apparatus of a humble-bee (*Bombus hortorum* L. ♀) in a middle sucking position (7 : 1).

When drawn back into the extremity of the tubular mentum, as is shown in Fig. 3, the tongue by no means overtops the labial palpi, but is wholly enclosed by them from beneath, whilst when pulled out as far as possible (as shown in Figs. 1, 2, and 4) it considerably overtops the labial palpi. The base of the mentum is inserted in a horny ridge, called by Kirby (in his "Monographia Apum Angliæ") the *fulcrum* (*f*). The fulcrum is placed at the conjunction of two diverging horny ridges, called by Kirby *cardines* (*c*), which connect the base of the fulcrum with the basal portion or *stipes* (*st*) of the maxillæ. The cardines can be turned round their food-points; when turned forwards, they also push forwards the fulcrum and the mentum, so as to overtop considerably the basal portion of the maxillæ (as shown Figs. 1, 2); when turned backwards, they also draw backwards the parts inserted in them, and the mentum is now enclosed by the basal portion of the maxillæ (as shown in Fig. 4). In this position the terminal portions of the two maxillæ, the *laminæ* (*la*) appearing as two flattened, lanceolate, horny pieces with a central rib, form a sheath to the tongue enclosing it from above, whilst at the same time the two first joints of the labial palpi enclose it from beneath. The *maxillary palpi* (*mp*) exist in the mouth of typical bees only as atrophied useless organs.

Besides the two foldings hitherto explained, two other foldings are to be mentioned. First, the whole apparatus hitherto described is inserted in the terminal points of two long, horny ridges enclosed in the excavation of the head and moveable round their food-points (*l*, *lora*, of Kirby). When turned forwards, the lora push forward to twice their own length the maxillæ and the mentum, with all their appendages; when turned backwards, they draw them backwards the same distance. Secondly, when all three withdrawals hitherto mentioned—(1) of the base of the tongue, (2) of the cardines, (3) of the lora—are effected, the mentum lies, defended on each side by the basal portion of the maxillæ (*st*), enclosed in the excavation of the under-side of the head; only the tongue sheathed by the laminæ and the labial palpi overtop the head, and prevent the jaws from being used; but all these overtopping parts are bent downwards and backward very easily; and now the jaws or *mandibulæ* (*md*) are not prevented from being employed.

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[*] C. Vogt, Zool. Briefe i. p. 678.

[†] Grundzüge der Zoologie, 1866, p. 323.

The separate parts of the mouth of the bee and their power of moving having been considered, it remains to examine what use the bee makes of them in its different actions.

1. In order to empty the deepest honey tubes accessible to it, the bee stretches out all the moveable parts of its sucking apparatus (lora, cardines, laminæ, maxillar palpi, and tongue) in the same manner as is shown in Figs. 1 and 2, with the only difference that the two first joints of the labial palpi sheathe the tongue from beneath, and that the laminæ closely embrace the mentum and the basal part of the tongue from above. Then the terminal hairy whorls of the tongue, protruded as far as possible and advanced to the bottom of the honey-tube, being wetted with honey, the bee, turning backwards the cardines (*c*), withdraws the mentum, together with the tongue and the labial palpi, so far that the laminæ are no longer overtopped by the labial palpi, and that the laminæ and the labial palpi together, closely embracing the tongue, form a sucking-pipe, of which only the part *k-l* (Fig. 4) of the tongue is prominent. But almost at the same time the bee, folding the base of the tongue into the tubular extremity of the mentum, withdraws the terminal hairy whorls wetted with honey into the sucking-pipe, in which the honey is forthwith driven downwards to the oral opening by the erection of the whorls of hairs progressing quickly from the tip of the tongue towards its base, and simultaneously by the enlargement of the interior abdominal hollows connected with the œsophagus, which are visible from the outside by the swelling of the abdomen, and which must suck the honey towards the œsophagus.

Fig. 4 shows the head of a humble-bee in a medium sucking position. When from this position the base of the tongue is folded into the hollow extremity of the mentum (as illustrated by Fig. 3), the part *k-l* of the tongue wetted with honey is withdrawn into the sucking-pipe. Now when the lora (*l* in Fig. 4, directed downwards) are turned backwards round their food-points, the base of the sucking pipe (near *mp* Fig. 4) is withdrawn to the opening of the mouth (between the base of the two mandibulæ, *md* and the labrum, *lbr*, Fig. 4, below the epipharynx *ep*, Fig. 1), and the honey is, by pressing and sucking, driven to the œsophagus. When the lora (*l*) are again turned forwards, the whole sucking apparatus is pushed forward double the length of the lora; and now the cardines turning forward, the mentum with its appendages again advances double the length of the cardines, while the maxillæ remain at the same place, and the laminæ from this cause embrace only the mentum and the basal portion of the tongue; when at last the base of the tongue infolded in the tubular mentum is stretched out, the tongue is again protruded to its fullest extent, and the terminal whorls of hairs are again wetted with honey at the bottom of the honey-tube of the flower.

In a flower rich in honey, a humble bee may be observed executing four, five, and sometimes more, even eight or ten separate acts of suction, probably accompanied by as many protrusions of the tip of the tongue into the honey, and withdrawals of it and of the whole sucking-pipe.

I am fully convinced that the movements of the oral apparatus of the bees are as described; for by intoxicating honey- and humble-bees by chloroform, and immersing the tip of their tongue into a solution of sugar, I sometimes succeeded in seeing the movements described performed sufficiently slowly to discern each separate act very well. What occurred within the sheath of the tongue formed by the laminæ and the maxillary palpi, was of course not visible, but bending them aside after wetting the tip of the tongue with the solution of sugar, I sometimes saw the erection of the whorls of hairs progressing from the tip towards the base of the tongue.

Hence undoubtedly the statement of zoologists, who, absolutely denying the sucking power of bees, assert that they lick or lap the honey in a manner similar to a dog or a cat when drinking, must be essentially modified. The terminal whorls of hairs are filled with honey by adhesion; this honey withdrawn into the sheath of the tongue is driven towards the œsophagus by a double cause, first by the pressure of the erect whorls of hairs, and secondly by suction.

HERMANN MÜLLER

(*To be continued*)

ON SOME REMARKABLE FORMS OF ANIMAL LIFE FROM GREAT DEEPS OFF THE NORWEGIAN COAST*

THE name of George Ossian Sars is honourably connected with a very interesting chapter in the history of deep-sea research. As early as 1850, his illustrious father, Dr. Michael Sars, had challenged Edward Forbes's conclusions respecting the bathymetrical terminus of animal life. He remarked,† that at least in the Norwegian Seas, it appeared to extend much beyond the limit which the English naturalist had fixed for it. Forbes had not dredged below 230 fathoms, and at this depth he had only obtained two living Mollusca and a couple of Serpulæ; hence he was led to place the zero of animal life at 300 fathoms. Sars, on the contrary, even at the early period just mentioned, had obtained from a depth of 300 fathoms a number of animals, including a species of Coral, Molluscs, Polyzoa, &c.; and he sagaciously remarked that there was evidence of the existence of a *vigorous* animal life at this great depth, inasmuch as some of the species (*e.g. Terabratula septigera* and *Lima excavata*) were the largest known representatives of their respective genera. In confirmation of his opinion, he was able to offer, in 1864, a Catalogue of 92 animals, which had been obtained in depths varying from 200 to 300 fathoms. More recently his son has devoted himself with much energy and success to deep-sea investigation, and in 1868 had extended his dredgings to 450 fathoms, and added no less than 335 species to those already published. He says:—"I found to my great surprise at this enormous depth, not . . . a poor and oppressed Fauna, but on the contrary a richly developed and varied animal life. . . . And so far was I from observing any sign of diminished intensity in this animal life at increased depths that it seemed, on the contrary, as if there was just beginning to appear a rich and in many respects peculiar deep-sea fauna, of which only a very incomplete notion had previously existed." Amongst the new forms thus obtained was the famous *Rhizocrinus Lofotensis*, descended from Oolitic ancestry, which furnished, according to Dr. Carpenter, "a principal 'motive'" of the *Lightning* expedition. It is interesting to learn that these productive dredgings at the great depth of 200-450 fathoms were accomplished in an ordinary fishing-boat with a crew of three men.

In the important paper which forms the subject of the present notice, Mr. G. O. Sars has given us an account of some of the results of his dredgings in the "great deeps" off the Coast of Norway, founded partly on the posthumous manuscripts of the late Prof. Sars, and partly on his own investigations. Various new species of Mollusca, Annelids, Corals, and Sponges, all of them dwellers in depths varying from 100 to about 500 fathoms, are described, and illustrated by excellent figures. But that which gives a peculiar and distinctive interest to the work is the elaborate memoir on a remarkable Polyzoon, taken in the year 1866, from a depth of 120 fathoms, at Skraaven, in Lofoten. This unique animal is not only

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* Partly from posthumous manuscripts of the late Prof. Dr. Michael Sars By George Ossian Sars.

† "Beretning om en i Sommerenn, 1849, foretagen Zoologisk Reise i Lofoten og Finmarken," p. 13.